CLASSIFICATION OF THE LORANTHACEAE AND VISCACEAE.

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Synopsis.

The commonly recognized subfamilies Loranthoideae and Viscoideae of the Loranthaceae *sens. lat.* are accepted as distinct families Loranthaceae and Viscaceae respectively. The two families differ in many features of floral morphology, floral anatomy and embryology. The features which the two families have in common are features occurring elsewhere in the order Santalales and especially in the family Santalaceae, and the Loranthaceae and Viscaceae are the result of independent, convergent evolution towards aerial parasitism.

Introduction.

The Loranthaceae (*sens. lat.*) are a group with several very distinctive features, including considerable reduction and modification in ovary structure and a specialized hemiparasitic habit. The group consequently has been the subject of several monographic treatments, and most authors have regarded the common features of floral structure and life form as evidence that it constitutes a single family. Several authors have suggested, however, that the two widely accepted subfamilies Loranthoideae and Viscoideae are independent groups and recent studies, particularly in ovary development and embryology, support this view. Two families, Loranthaceae and Viscaceae, have thus been recognized.

The recent authors who have accepted this treatment have not been concerned with taxonomic revision and have not provided formal diagnoses of the two families. The present author recognizes the independence of the two groups and considers it desirable to redescribe the families so as to incorporate the additional information which has become available since the first description of the Viscaceae more than a century ago. The following classification of the Loranthaceae and Viscaceae is proposed and has been adopted in taxonomic revisions which are in preparation. Further discussion of the proposed system is presented below.

Classification of the Loranthaceae and Viscaceae.

A. Viscous layer of the fruit within the vascular bundles. Embryo sac single, of the allium type. Suspensor of the embryo absent or very short ..... Family VISCACEAE.
I. Anthers 4-celled. Placenta basal. Inflorescence a simple raceme or spike ..... Tribe Eremolepideae Tiegh.
a. Leaves alternate. Seeds with endosperm ..... Subtribe Eremolepidinae Engl.
b. Leaves opposite. Seeds without endosperm ..... Subtribe Lepidoceratinae Engl.
II. Anthers 2-celled. Placenta central. Embryo sac U-shaped, growing into the ovary tissue ..... Tribe Phoradendreae Tiegh.
a. Inflorescence a spike of triads. Anthers not cohering ..... Subtribe Ginalloinae Engl.
b. Flowers in groups at the nodes. Anthers cohering .... Subtribe Korthalsellinae Engl.
c. Flowers in groups on the internodes. Anthers not cohering ..... Subtribe Phoradendrinae Engl.
III. Anthers 1-celled. Placenta central. Embryo sac straight, ascending within the placental column ..... Tribe Arceuthobieae Tiegh.
IV. Anthers many-celled. Placenta basal. Inflorescence an axillary cyme or raceme of cymes ..... Tribe Visceae Tiegh.
B. Viscous layer of the fruit outside the vascular bundles. Embryo sacs several, of the polygonum type. Suspensor of the embryo very long, multiseriate ..... Family LORANTHACEAE.

I. Placental column (mamelon) with 3-6 basal lobes and the sporogenous cells in the lobes. Ovary often 3-6-celled in the lower part. Embryo sacs confined to the mamelon. Fruit drupaceous or baccate ..... Tribe ELYTRANTHEAE Dans.
a. Fruit drupaceous. Pollen spherical. Terrestrial root-parasitic trees or shrubs ..... Subtribe GAIADENDRINAE Engl.
b. Fruit baccate. Pollen trilobate. Aerial stem-parasitic shrubs ..... Subtribe ELYTRANTHINAE Engl.
II. Placental column (mamelon) with 4 basal lobes containing the sporogenous cells. Ovary 4-celled in the lower part. Embryo sacs ascending more than half-way up the style. Fruit dry, tripterous. Pollen trilobate. Terrestrial root parasitic trees ..... Tribe NUYTSIEAE Tiegh.
III. Placental column (mamelon) simple or absent, with the sporogenous cells in a single central mass. Ovary always 1-celled. Embryo sacs ascending in the style. Fruit baccate ..... Tribe LORANTHEAE Engl.
a. Seeds with endosperm ..... Subtribe LORANTHINAE Engl.
b. Seeds without endosperm ..... Subtribe PSITTACANTHINAE Eng.

VISCACEAE Miq.

Fl. Ind. Bat., 1, 1 (1856) 803; Miers, *Contrib. Bot.*, (1851) 39 (*nom. provisorium*); *Ann. Mag. Nat. Hist.*, 8 (1851) 179 (*nom. provisorium*); Agardh, *Theoria Syst. Plant.*, (1858) 114; (-acées) Tiegh., *Bull. Soc. bot. Fr.*, 43 (1896) 247, 544; Maheshwari, Johri & Dixit, *J. Madras Univ.*, B, 27 (1957) 134; Johri & Bhatnagar, *Proc. Nat. Inst. Sci. India.* 26, B (1961) 215; Johri, *Recent Adv. Emb. Angio.* (1963) 410; Loranthaceae subfam. Viscoideae Engl. *Pflanzenfam.*, 3, 1 (1889) 177; (-oidées) Tiegh., *Bull. Soc. bot. Fr.*, 41 (1894) 138; Dans., *Bull. Jard. bot. Buitenz.*, 11 (1931) 236; Viscales Tiegh., *Bull. Soc. bot. Fr.*, 43 (1896) 247; Arceuthobiacées, Ginalloacées Tiegh., *Bull. Soc. bot. Fr.*, 43 (1896) 543, 544; *Compt. Rend. Acad. Sci. Paris*, 124 (1897) 656; Lepidariacées, Razoumovskiacées, Eremolepidacées Tiegh., *Compt. Rend. Acad. Sci. Paris*, 150 (1910) 1717, 1718.

Flowers minute (usually less than 2 mm. long), monochlamydeous, unisexual. Perianth segments 2 to 4, valvate. Stamens opposite the perianth segments, adnate to them or free; anthers 1- to many-celled, opening by pores; pollen spherical. Ovary inferior, 1-celled, with a short placental column containing the sporogenous cells; ovules absent; embryo sac single, developing from one cell of a dyad (allium type), confined to the placental column or extending into the adjacent ovary tissue. Fruit baccate, the viscous layer within the vascular bundles; cleavage of the zygote usually transverse; suspensor absent or very short. Hemiparasitic shrubs on the branches of trees; haustorial attachment single, without runners. Leaves mostly opposite and curvinervous, occasionally alternate or absent.

The Viscaceae include 11 genera and about 450 species, of which the largest genera are *Phoradendron* (about 250 spp. in America), *Viscum* (about 65 spp. in the Old World) and *Dendrophthora* (about 60 spp. in Central and South America). The family is widespread in all continents but has its richest development in tropical and subtropical areas. It is poorly represented in Australia, where *Viscum* (5 spp.), *Notothixos* (4 spp.) and *Korthalsella* (2 spp.) are largely confined to the northern and eastern coastal and subcoastal districts.

Infrafamilial categories. The Viscaceae (as Loranthaceae Viscoideae) have had a relatively stable taxonomic history and there has been general agreement among authors on classification within the group. The treatment adopted here is that of Engler and Krause (1935), without any change in rank in the infrafamilial categories. In view of the incomplete knowledge of floral structures and reproductive processes, modification of the system would be premature at this stage. In any case the present data conform fairly closely with the current system and show reasonable uniformity within the family, and the recognition of subfamilies may not be justified.

LORANTHACEAE D. Don.

Prodr. fl. nepal., (1825) 142; Miq., *Fl. Ind. Bat.*, 1, 1 (1856) 807; Agardh, *Theoria Syst. Plant.*, (1858) 117; (-acées) Tiegh., *Bull. Soc. bot. Fr.*, 43 (1896) 247; Loranthaceae subfam. Loranthoideae Engl., *Pflanzenfam.*, 3, 1 (1889) 177; (-oidées) Tiegh., *Bull. Soc. bot. Fr.*, 41 (1894) 138; Dans., *Bull. Jard. bot. Buitenz.*, 11 (1931) 235; Loranthales

Tiegh., *Bull. Soc. bot. Fr.*, 43 (1896) 247; Elytranthacées, Nuytsiacées Tiegh., *Bull. Soc. bot. Fr.*, 43 (1896) 247; Dendrophthoacées, Treubellacées Tiegh., *Bull. Soc. bot. Fr.*, 43 (1896) 543; *Compt. Rend. Acad. Sci. Paris*, 124 (1897) 656; Nuytsiales, Elytranthales Tiegh., *Compt. Rend. Acad. Sci. Paris*, 150 (1910) 1716; Lepidariacées, Gaiadendracées, Treubaniacées Tiegh., *Compt. Rend. Acad. Sci. Paris*, 150 (1910) 1717, 1718.

Flowers mostly more than 5 mm. long, dichlamydeous, hermaphrodite or, when unisexual, mostly dioecious. Calyx reduced to a lobed or truncate limb at the apex of the ovary, without vascular bundles. Corolla polypetalous or gamopetalous, usually actinomorphic, consisting of 4–12 segments, valvate. Stamens as many as the petals, opposite them and epipetalous; anthers primarly 2- or 4-celled (sometimes with transverse partitions), mostly basifixed and immobile but sometimes dorsifixed and then usually versatile, opening longitudinally; pollen mostly trilobate, rarely triangular or spherical. Ovary inferior, 1- to several-celled, with or without a central placental column (mamelon); ovules absent; sporogenous tissue massive, located in the mamelon or at the base of the ovarian cavity; embryo sacs several, developing from one cell of a tetrad (polygonum type), considerably elongated, confined to the mamelon or ascending in the style, and developing basal caeca which reach a collenchymatous pad at the base of the ovary. Fruit mostly baccate (rarely dry or drupaceous), the viscous layer, when present, outside the vascular bundles; cleavage of the zygote vertical; suspensor long, biseriate; endosperm compound. Hemiparasitic terrestrial root-parasitic shrubs or trees, or aerial stem-parasitic shrubs. Leaves mostly opposite.

The Loranthaceae *sens. str.* include about 65 genera and 850 species, and are well represented in the tropics of both hemispheres, with a lesser number of species in temperate habitats. The Loranthaceous floras of Africa, Asia-Australasia and America are all rather different in character and the three areas represent major secondary centres of development. The family is represented in Australia by 12 genera (seven of them endemic) and about 65 species, and is distributed throughout the mainland.

Infrafamilial categories. The taxonomic proposals of Danser (1933) for the family have been widely accepted. Further anatomical and embryological investigations may necessitate modification of the scheme, but it is proposed for convenience to follow Danser's system, without change in rank, at this stage. On the basis of ovary structure (Narayana, 1958) tribe Nuytsieae probably should be reduced to a subtribe of Elytrantheae. The distinction of subtribe Psittacanthinae on the absence of endosperm is probably not justified (MacBride, 1937), and the group is probably unnatural.

Discussion.

Miers (1851*a*) drew attention to the differences distinguishing *Viscum*, which was then taken in a broad sense, including the present genus *Phoradendron*, from the remainder of the Loranthaceae. The differences included the minute flower size, the unisexual, monochlamydeous flowers, the almost sessile anthers opening by pores and the sessile, clustered flowers. Miers also noted that *Viscum* had spherical pollen whereas that of the Loranthaceae available to him was trilobate. He considered *Viscum* to have a close affinity with the Santalaceae but regarded the remaining Loranthaceae as being more closely related to the Proteaceae. Miers proposed the raising of *Viscum*, together with *Lepidoceras* and *Myzodendron*, to family rank as the Viscaceae, but as an alternative suggested that they may be treated as a subfamily of the Santalaceae, thereby invalidating his description of the family Viscaceae. Miers' views were repeated soon afterwards in a second article on the same topic (Miers, 1851*b*). Miquel (1856) accepted Miers' first proposal and gave detailed descriptions of the Loranthaceae (*sens. str.*) and Viscaceae, attributing the latter name to Miers. A family Viscaceae was also recognized and described by Agardh (1858), who based his conclusions on floral characters but made no reference to the works of the earlier authors. The recognition of a family Viscaceae by Van Tieghem (1896*a*, *b*, 1897, 1910) was due to his use of new criteria for classification of the angiosperms and has little bearing on the present treatment.

Even though Miers', Miquel's and Agardh's conclusions were based on a limited range of material, there are few exceptions known to the criteria on which they distinguished the families, and each appears to be a relatively uniform group within itself. In the Loranthaceae the few occurrences of unisexual flowers are in distantly related groups and are presumably of independent origins. Small flowers (less than 10 mm. long) are rare and in one American genus only are they of the minute size of the Viscaceae. Spherical pollen in the Loranthaceae is known only in *Atkinsonia* and *Tupeia* and in each case the grains have distinctive features and show little evidence of a closer affinity with the Viscaceae than with other groups in the Santalales. Only in the male flowers of *Tupeia* is a truly monochlamydeous condition known in the Loranthaceae.

These differences between the two groups could thus be considered to justify their treatment as distinct families although the work of the earlier authors was largely overlooked. Most recent support for this approach, however, has arisen from embryological studies (Maheshwari, 1954, 1958; Maheshwari, Johri and Dixit, 1957; Johri and Bhatnagar, 1961), which have demonstrated several other differences in flower development and fruit structure, and Johri and his co-workers have adopted this treatment in several embryological reports (cf. Johri, Agrawal and Garg, 1957). In the Viscaceae the embryo sac is single, of the allium type (cf. Maheshwari, 1950), and is confined to the placental column or adjacent ovary tissue. The embryo sacs in the Loranthaceae are several, of the polygonum type; they elongate into the style and they develop caeca from the lower ends which reach a collenchymatous pad or tube at the base of the ovary. The first cleavage of the zygote in the Loranthaceae is vertical, and the embryo is pushed downwards by a long biseriate suspensor into a compound endosperm formed from several embryo sacs. In the Viscaceae the zygote commonly cleaves transversely, the suspensor is small or absent, and the endosperm is not composite. The two families are also distinguished constantly by the positions of the viscous layer in the fruit, being outside the vascular bundles in the Loranthaceae and within them in the Viscaceae, so that the mechanism for bird dispersal may have arisen independently in each group.

Most of the characters which the two families have in common are also features of the Santalaceae, where hemiparasitism is common (mostly root parasitism) and there are various degrees of reduction and suppression of ovules and elongation of embryo sacs (Johri and Bhatnagar, 1961). It is most likely that the two groups have had independent origins from ancestral stocks in the Santalaceae, so that by placing them in a single family they constitute a diphyletic and therefore unnatural group. The "new" characters which the groups share are the aerial habit, which in fact has been discovered in other families of Santalales and which therefore has probably originated several times, and the baccate fruits, which are a consequence of the aerial habit and of independent development.

The basic chromosome number of the Loranthaceae (*sens. str.*) is n = 12 (Barlow, 1963). Polyploidy appears to be entirely absent and chromosome evolution has involved progressive aneuploid reduction to n = 8, the various basic numbers conforming with taxonomic grouping and degree of advancement. In the Viscaceae fewer numbers are known, but the basic number is apparently higher and chromosome evolution independent. A low frequency of polyploidy is known in the Viscaceae (Barlow, 1963, 1964). The few known numbers of the Santalaceae (Darlington and Wylie, 1955; Love and Love, 1961) indicate a greater range of basic numbers and a higher incidence of polyploidy and secondary diploidy, which conforms with the suggestion that the Loranthaceae and Viscaceae have arisen from cytologically different stocks.

The Loranthaceae and Viscaceae are thus relatively uniform groups characterized by a high degree of reduction in the ovary and by a hemiparasitic habit, these being features also of the Santalaceae, from which they have independently arisen. While it is possible that further investigations may demonstrate independent groups within these taxa, the present treatment is considered the most satisfactory reflection of their phyletic position.

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